

## Compare the rôles of the retina and central neurons in the analysis of visual input.

When light impinges on the retina, it is detected by the photoreceptors and then processed by bipolar, horizontal and amacrine cells before being converted into a frequency-modulated train of action potentials in ganglion cells. The retinal processing system is organized to do a great deal of analysis as early as possible, at the point where maximum information is available; the result of this processing is the output from the ganglion cells. All the cells in the pathway before the ganglion cell transmit information not by using action potentials but by varying their rate of neurotransmitter release in response to fluctuations in their membrane potential. This enables information to be preserved as far as possible: frequency coding at this stage (with a neuron's maximum of about 1kHz) would drastically reduce the sensitivity of the system, and the distances are as yet short enough that signal decay along the length of a cell is not significant.

**Ganglion cells** fall into three categories in primates: M, P and W cells. **W (wide field) cells** are few in number and have a simple large circular receptive field (the area of the retina to which they can respond). They respond slowly and tonically, and their response is proportional to the light intensity on the receptive field. They project to the lateral geniculate nucleus of the thalamus (LGN), the superior colliculus, the pretectum and the suprachiasmatic nucleus of the hypothalamus<sup>1</sup>, and are involved in simple functions such as localisation, control of pupil size and entrainment of circadian rhythms. The other types, M (magnocellular) and P (parvocellular), both have a circular receptive field that consists of a centre and a surround. **M cells** are large and have large receptive fields; they show brisk transient responses, project to the LGN and superior colliculus and are mostly concerned with movement detection. **P cells** are more numerous and are medium-sized, firing briskly but tonically in response to light; they project only to the LGN and are concerned with spatial analysis (fine detail) for the recognition of objects. They are mostly wavelength-selective and involved in colour vision.

Both M and P cells have a **centre** and a **surround** to their receptive fields, as described. They can be further subdivided into cells excited by light to their centre (*on-centre*) – these cells are inhibited by light to their surround. Diffuse light excites them but little, as the inhibition from the surround largely cancels the excitation from the centre. In contrast, *off-centre* ganglion cells have the precisely opposite arrangement, and thus their spontaneous firing is suppressed by light to their centre, but accelerates for a time after the light is turned off (hence the name). These properties are a result of simple arrangements of the retinal interneurons which collect information over the area of a ganglion cell's receptive field and create the centre/surround division by means of **lateral inhibition**. In the dark-adapted eye these properties are lost, with the result that the information-processing properties of the retina are sacrificed for sensitivity in light detection: the ganglion cells act purely as light detectors.

From the properties described one can see what information is extracted from the visual scene. **The centre/surround organisation enables the visual system to respond primarily to contrast**. The ganglion cells function as contrast detectors (edge detectors), because they are excited (or inhibited) best by a stimulus which covers their centre but not their surround. Physiologically this is important, because it is the contrast in a scene that is largely independent of ambient light intensity, and which is determined by the properties of objects being viewed. The processing is best done in the retina because at this stage small differences in light intensity can be detected by the neurons; once the information is frequency-coded, such small differences would be undetectable; the ganglion cells encode the *differences* between light intensities. **The parallel on-centre and off-centre neuron systems allow improved sensitivity to temporal changes in light intensity**. An on-centre neuron responds well (by increasing its firing rate) to increased illumination, but as its spontaneous firing rate is low it responds relatively little to decreased illumination (the rate falls to zero and no farther!). On the other hand, an off-centre neuron is capable of a sensitive response to decreased illumination of its centre, as this excites it to fire.

The **LGN** appears not to process visual information at all in any obvious way. Its relay cells have the same responses to light as the retinal ganglion cells, so its function is obscure. However, only 10-20% of the presynaptic connections onto these cells are from the retina. Among the rest are feedback connections from the reticular formation and cortex; this input may control ('gate') the information flow from retina to cortex.

The first relay point at which receptive field properties change significantly is the **primary visual cortex**. There is a complex system of local excitatory circuits, inhibitory feedback and lateral spread of information in the layers of the cortex that processes the incoming information. As a result, only the 'blob' zones concerned with colour processing have cells with circular receptive fields. The rest respond to **linear stimuli** (lines or bars) and are classified as simple or complex.

**Simple cells** have receptive fields whose on/off zones are larger than LGN cells, and have rectangular receptive fields with a specific axis of orientation. Some have rectangular on-centres that are flanked by off-surrounds;

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<sup>1</sup>I assume the SN innervation is by W cells, at any rate

some the opposite; some have one 'on' and one 'off' region next to each other. The effective on-stimulus for the {on-centre, flanked off-surrounds} type cell must excite a particular area of the retina, have the correct linear properties (here, a bar) and be of the correct orientation (the most effective stimulus obviously coincides with the subdivisions of the receptive field). Other cortical cells receiving input from the same area of retina have similar field shapes but different orientations, so **every axis of rotation is represented for every retinal position**. The rectangular fields are built up by simple combination of circular fields from LGN cells.

**Complex cells** usually have larger receptive fields than simple cells. They also **have a critical orientation axis but the precise position within the field is unimportant**. They respond particularly well to movement of a correctly-oriented stimulus across the receptive field. This response is probably built up from simple cortical cells that share a common orientation but have slightly offset field positions.

Simple and complex cells are likely important for **analysing the contours and boundaries of visual images in terms of line segments**. Also, the interaction between simple and complex cells may be important for the constancy of perception of form despite small head or eye movements: small displacements of an image on the retina will excite different populations of simple cells but the same population of complex cells<sup>2</sup>. This is known as **positional invariance**.

Another important property of this analysis is that it reduces the amount of information that must be transmitted to higher centres. For example, if a dark square on a light background is presented, the constant colour or shade of the square and background can be largely ignored by transmitting the information as "four lines, thus... dark within, light without". **The cells of the visual system pay much more attention to the outlines of an object than its interior**.

It can also be seen from the description so far that at each level of visual processing, cells have a greater capacity for *feature abstraction* than cells at lower levels. In addition to the analysis described, there is further parallel processing in the form of the magnocellular and parvocellular pathways from the LGN: the magnocellular input is concerned more with movement and coarse outlines while the parvocellular input is concerned more with colour, texture and pattern. Both could contribute to an initial 2-D representation of stimulus shape and contour (the "primal sketch") within the cortex. Also within the primary visual cortex are cells that respond to binocular retinal disparity, so the first hints of 3-D processing are present.

At higher levels still, in the visual association cortex, images are processed to give a representation of the world around us in terms of three-dimensional objects in space. This involves discriminating objects from background; interpreting 2-D images as 3-D by their patterns of light and shade; determining objects' size by monocular and binocular distance cues and so on. At this level neural processing is poorly understood. However, it is thought that vision is mediated by three parallel pathways for motion, depth and form, and colour. These pathways have been characterised anatomically, and regions of the brain specialised for recognising physiologically important stimuli found (such as for faces in a monkey, or a sheep's horn length in sheep, or sheep's faces looking directly at the viewing sheep). The region of the brain responsible for creating a map of the body and other objects in space has also been found: it is believed to be the posterior parietal cortex. At this level it seems reasonable to assume that the neurons are in the "vicinity" – if such a term is really appropriate – of conscious attention; however, this is even less understood!

Vision is of great importance in primates in providing an internal representation of the physical world, and so a great deal of neural processing is associated with it. Much of it is not understood, but the simpler levels of processing have been well characterised. To summarise, the retina itself detects light and sends information on contrast and temporal changes in light intensity to the LGN. The LGN may gate the information passing through it, giving it the potential to be involved in visual attention. The primary visual cortex processes information as colour blobs and line segments, stationary and moving, and the visual association cortices synthesise this information into a four-dimensional map (position and movement) of recognised objects.

[RNC, unmodified 1994, 1650 words.]

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<sup>2</sup>By this argument one might expect either (a) cells that were independent of orientation (to detect form as invariant despite small *rotations* of the object/eye/head), or (b) perceptual differences between translation and rotation of objects. Is one or both of these true?